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Convergent Evolution of Vertical Movement Behavior in Swordfish, Bigeye Tuna, and Bigeye Thresher Sharks

Vertical Niche Partitioning in the Pelagic Environment as Shown by Electronic Tagging Studies

Michael K. Musyl, Lianne M. McNaughton, J. Yonat Swimmer and Richard W. Brill

We are using acoustic, archival, and pop-up satellite archival tags (PSATs) to study vertical and horizontal movement patterns in commercially and ecologically important tuna, billfish, and shark species, as well as sea turtles. The work is part of a larger effort to determine the relationship of oceanographic conditions to fish and sea turtle behavior patterns. This information is intended for incorporation into population assessments, addressing fisheries interactions and allocation issues, as well as improving the overall management and conservation of commercially and recreationally important tuna and billfish species, sharks and sea turtles.

The research, sponsored by the Pelagic Fisheries Research Program and the NOAA Fisheries-Pacific Islands Fisheries Science Center, has shown that some large pelagic fishes have much greater vertical mobility than others. More specifically, we have found that swordfish, bigeye tuna and bigeye thresher sharks remain in the vicinity of prey organisms comprising the deep Sound Scattering Layer (SSL) during their extensive diel vertical migrations. In contrast, other billfish, tuna and shark species stay in the upper 200 m of the water column both night and day (Figs. 1, 2, 3).

The SSL is comprised of various species of squids, mesopelagic fish, and euphausiids which undertake extensive diurnal vertical migrations. Pelagic fishes that are able to mirror movements of the SSL can better exploit these organisms as prey. Also, the ability of swordfish, bigeye tuna, and bigeye thresher sharks to access great depths permits them to effectively exploit the SSL for prey even after they descend to deeper water depths at dawn [e.g., over 500 m] (Fig. 4).

Certainly, the ability to mirror the movements of vertically migrating prey confers selective advantages. However, other pelagic species, such as, yellowfin tuna, silky sharks, oceanic white tip sharks, blue marlin, and striped marlin do not make extensive regular vertical excursions.

Recent studies of tuna trophic ecology near the main Hawaiian Islands (Grubbs and Holland 2003) have confirmed that bigeye tuna generally select mesopelagic prey from the SSL, while yellowfin tuna feed primarily on epipelagic prey from the mixed layer even when the fish are caught in the same areas.

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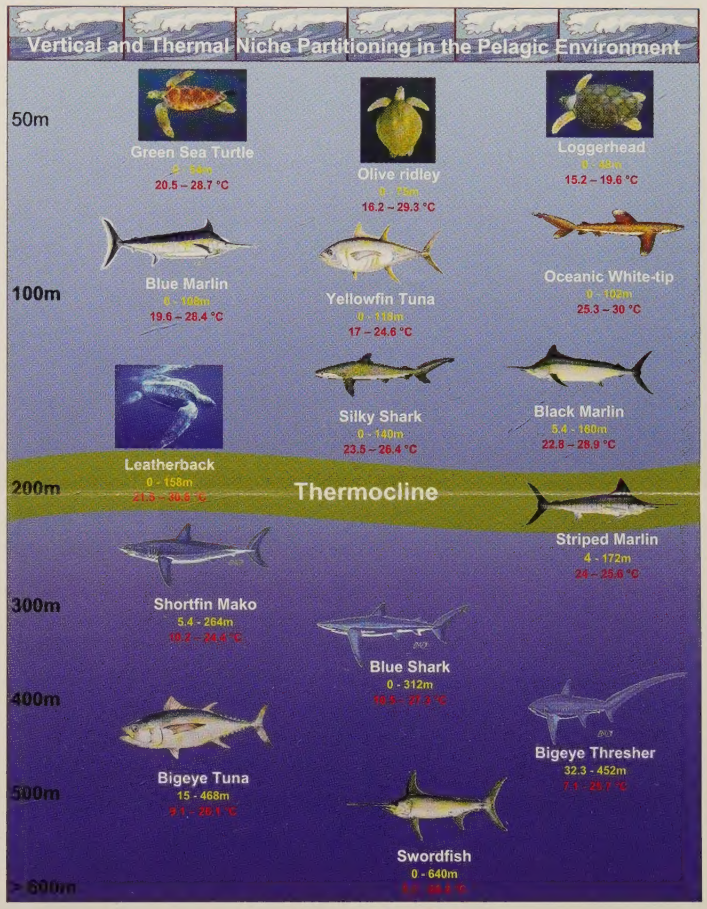

Figure 1. Values indicate the 95% depth and temperature preferences (combined day and night) for various pelagic species as indicated by electronic tagging studies funded by the Pelagic Fisheries Research Program of the University of Hawai'i, NOAA Fisheries, and Pacific Islands Fisheries Science Center.

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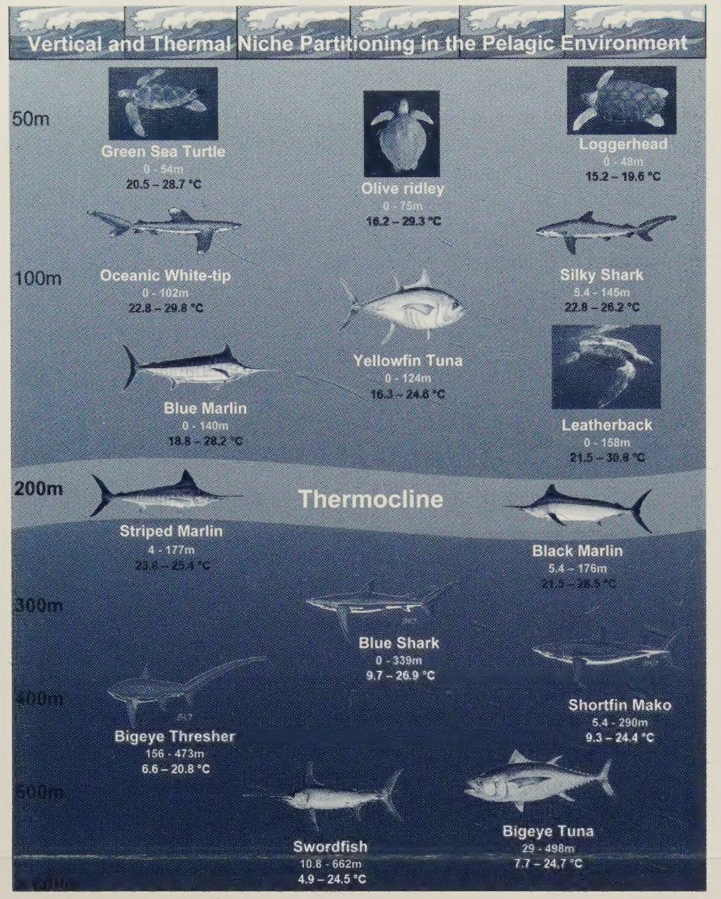

Figure 2. Values indicate the 95% depth and temperature preferences during the day for various pelagic species as indicated by electronic tagging studies funded by the Pelagic Fisheries Research Program of the University of Hawai'i, NOAA Fisheries, and Pacific Islands Fisheries Science Center.

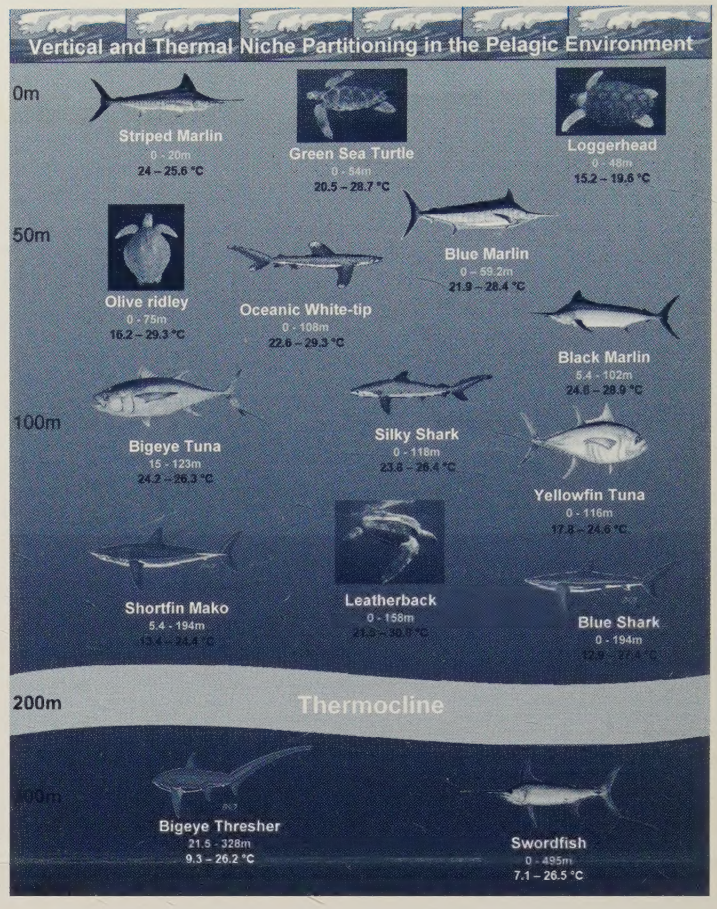

Figure 3. Values indicate the 95% depth and temperature preferences during the night for various pelagic species as indicated by electronic tagging studies funded by the Pelagic Fisheries Research Program of the University of Hawai'i, NOAA Fisheries, and Pacific Islands Fisheries Science Center.

We should point out that although the daily vertical movements of swordfish mirror the movements of the SSL, they are most likely following the vertical movements of larger cephalopods (the neon flying squid), which they exploit as a primary food resource. The larger squid, in turn, are following the movements of the SSL.

We have also found that one of the most ubiquitous large vertebrate species in the pelagic environment, the blue shark, occasionally displays vertical movement behaviors similar to those of swordfish, bigeye tuna, and bigeye thresher sharks (Fig. 1). Blue sharks appear to have no unique anatomical or physiological adaptations, and Carey and Scharold (1990) have characterized blue shark vertical movement patterns in terms of behavioral thermoregulation.

Nevertheless, our observations lead directly to the question, "Why are blue sharks so successful?" We hypothesize that at least part of the answer is their ability to undertake extensive daily vertical movements, which result in better forage utilization and more effective niche partitioning.

Scientists tagging a blue shark.

Childress and Nygaard (1974) have suggested that the organisms composing the SSL evolved the ability to migrate downward during the day into the cold oxygen minimum layer as a refuge against predation. Studies of crustaceans living in the cold oxygen minimum zone have shown that they are able to do so because of a suite of morphological, physiological, and biochemical adaptations.

However, bigeye tuna, swordfish, bigeye thresher sharks, and neon flying squid have likewise evolved physiological abilities to invade the SSL organisms' predator refuge. We view this situation as a sort of "physiological arms race." The parallel behaviors of both fish and organisms comprising the SSL adjusting their vertical movement patterns appear to strongly correlate with moon phase.

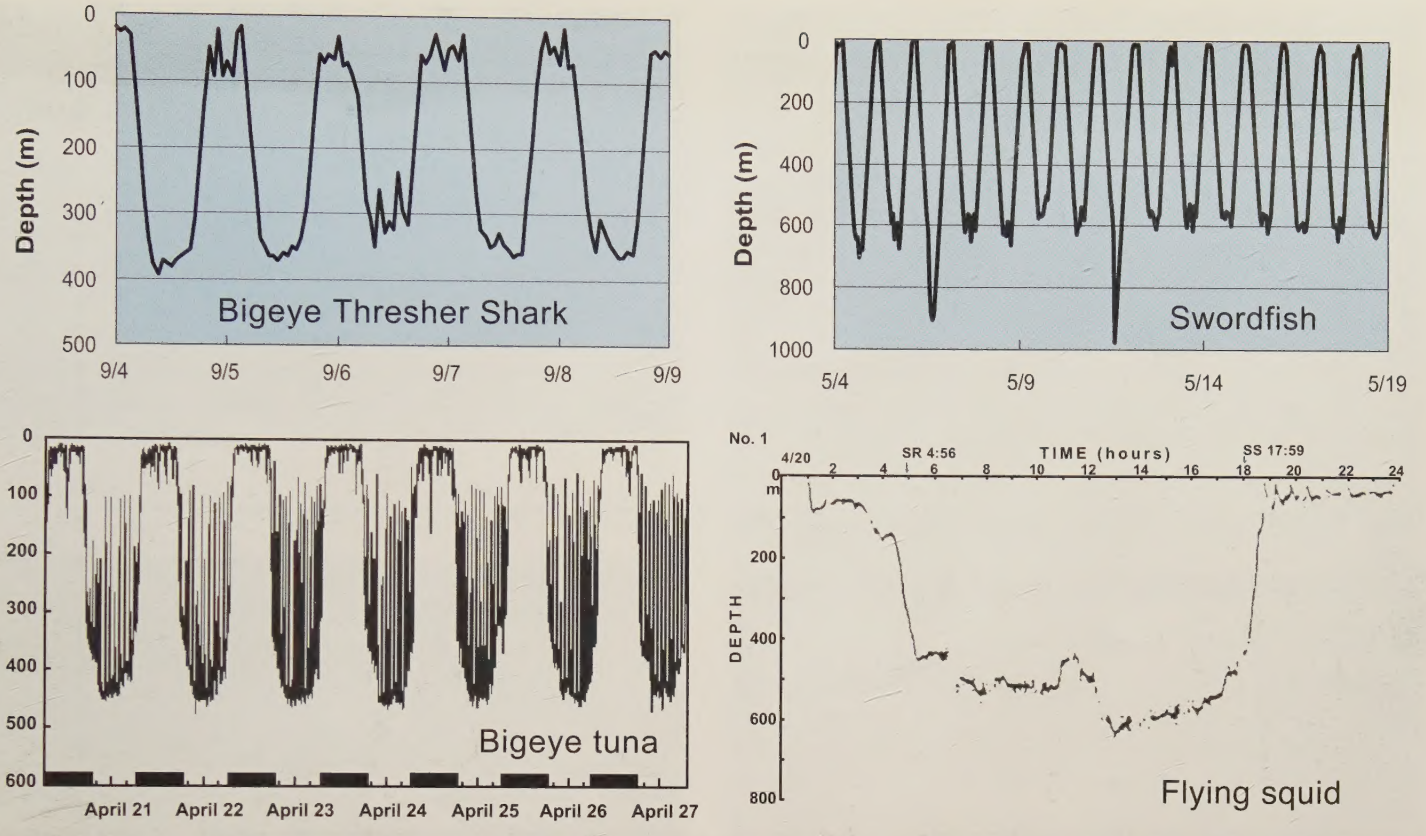

Figure 4. Illustrates the evident convergent dive patterns from disparate pelagic species. Note the regularity of the patterns and the "typical" pelagic behavior of diving deeper during the day and spending more time near the surface at night. Researchers believe this type of diving behavior evolved to mirror and exploit organisms comprising the Sound Scattering Layer.

For example, Musyl et al. (2003) demonstrated that adult bigeye tuna that were not associated with islands, seamounts, or FADs dramatically adjusted their nighttime dive patterns depending on the moon phase. That is, fish stayed deeper (ca. 80 m) during full moons and remained near the surface during new moons.

Researchers believe this behavioral modification helps "backlight" and silhouette prey organisms of the SSL. Furthermore, we suggest, as have others (e.g., Josse et al. 1998), that the vertical movements of large pelagic predators mirror the movements of their prey to the extent allowed by each species' physiology. Lastly, a logical hypothesis is to therefore suggest that the vertical distributions of pelagic fishes are influenced by both oceanographic conditions and the density and distribution of their prey.

We expect to continue this line of inquiry and to develop unique characters based on vertical movement patterns in order to examine the evolution of ecological relationships and vertical niche partitioning in the ocean. To aid in this endeavor, the following international team of collaborators has been assembled to investigate specific questions related to their area(s) of expertise:

- Fisheries Oceanography—Mike Laurs, Dave Foley, Keith Bigelow
- Habitat Based Stock Assessments—Pierre Kleiber, Keith Bigelow
- PSAT tagging studies and data analyses, pelagic fishes—Mike Musyl, Rich Brill, and Lianne M^{c}Naughton
- PSAT tagging studies and data analyses, marine sea turtles—Yonat Swimmer, Lianne M^{c}Naughton, Mike Musyl
- Fish Physiology—Rich Brill, Chris Moyes
- Individual Based Models—Hans Malte, Christina Larsen, Nini Jensen
- Sensory Physiology—Eric Warrant, Kerstin Fristches, Amanda Southwood
- Neural Anatomy—Tom Lisney
- Improvement of light-based geolocations—John Sibert, Anders Nielsen, Keith Bigelow, Mike Musyl
- PSAT Performance Evaluation—Geoff Arnold, Rich Brill, Mike Domeier, Molly Lutcavage, Mike Musyl, Yonat Swimmer, Steve Wilson
- PSAT and Archival database—John Sibert, Johnoel Ancheta, Dodie Lau, Mike Musyl

(continued on page 4)

Convergent Evolution (continued from page 3)

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Carey, F. G. and J. V. Scharold. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar. Biol.* 106, 329-342.

Childress, J. J. and M. H. Nygaard. 1974. The chemical composition and relative buoyancy of midwater crustaceans as a function of depth off Southern California. *Mar. Biol.* 27:225-238.

Grubbs, R. D. and K. N. Holland. 2003. Yellowfin and bigeye tuna in Hawai'i: dietary overlap, prey diversity and the trophic cost of associating with natural and man-made structures. *Proceedings of the 54th Annual International Tuna Conference*, Lake Arrowhead, California, 13-16 May 2003. SWFSC, NMFS, NOAA, La Jolla, CA.

Josse E., P. Bach, and L. Dagorn. 1998. Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia* 371/372:61-69.

Musyl, M. K., R. W. Brill, C. H. Boggs, D. S. Curran, T. K. Kazama, and M. P. Seki, 2003. Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. *Fish. Oceanogr.* 12:152–169.

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Fishery Monitoring and Economics Program

Preliminary Longline Logbook Summary Report

The Pacific Islands Fisheries Science Center presents its preliminary 2004 second quarter report for the Hawai'i-based longline fishery, "Fishery Monitoring and Economics Program Preliminary Longline Logbook Summary Report, April-June 2004" online at http://www.pifsc.noaa.gov/currentevents.html. Results are derived from the logbook data and are based on non-confidential summaries which provide:

- Fleet-wide analyses of effort, catch, and catch-per-unit effort, or CPUE
- A summary of logbook data
- Interactions with protected species
- Fishing effort
- Catch and targeted CPUE values for tuna, billfish, blue shark, and miscellaneous pelagic species
- Historical annual effort and catch figures on the Hawai'i-based longline fishery from 1991-2003

Federal longline logbook data for trips completed in the second quarter by Hawai'i-based longline vessel operators have been received and processed and are summarized in this report. There may be data from trips that began late in the second quarter and continued into the third quarter that are not presented herein. Therefore, this report should still be considered preliminary.

The Hawai'i-based longline fishery has operated under new rules since April 2, 2004. These new rules eliminate the southern area closure and reopen the swordfish-directed component of the fishery.

The swordfish component of the fishery will be subject to restrictions on effort, hook and bait types, and a separate annual total for interactions with leatherback and loggerhead sea turtles

A tuna longlining operation. Image courtesy of NOAA.

in order to minimize adverse impacts on sea turtles. Other mitigation measures, such as dehooking devices, also will be required. Swordfish effort and catch totals are expected to increase from the current low levels.

Preliminary longline logbook summaries show that 106 vessels made 330 trips in the second quarter of 2004, representing two less vessels and 40 less trips than in the same period of the previous year.

All trips targeted tuna. The total number of hooks set in this quarter was 7.5 million, up from the record high 6.8 million hooks set in the second quarter of last year. Most (70%) hooks were set outside the U.S. Exclusive Economic Zone (EEZ) along with the main Hawaiian Islands (MHI) EEZ (20%), the U.S. possessions (8%) and Northwestern Hawaiian Islands (NWHI) EEZ (2%).

Bigeye tuna catch (22,990 fish) in the second quarter of 2004 was almost double that in the same period last year; 72% of the bigeye tuna was caught outside the EEZ. Bigeye tuna CPUE on

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The Pacific Islands Fisheries Science Center of the National Marine Fisheries Service (NMFS) is part of the National Oceanic and Atmospheric Administration (NOAA). NOAA is one of the scientific research arms of the U.S. Department of Commerce. The center administers programs that support the domestic and international conservation and management of living marine resources.

The Pacific Islands Fisheries Science Center mission is linked to the NOAA Strategic Plan to build sustainable fisheries, recover protected species, maintain healthy living marine resource habitats, and manage international fisheries of highly migratory species in the Pacific (Department of State priority).

tuna targeted trips was 3.1 fish per 1000 hooks. Albacore catch (1,537 fish) and CPUE (0.2) were record lows for the second quarter.

Yellowfin tuna catch (3,151 fish) and CPUE (0.4) were less than half of the catch and CPUE last year.

Only 1,290 swordfish were caught in the second quarter 2004. Tuna-targeted swordfish CPUE in the second quarter was only 0.2

Striped marlin catch (2,727 fish) and CPUE (0.4) were well below last year. Blue marlin catch (1,375 fish) and CPUE (0.2) were substantially lower than the previous year.

A total of 13,548 sharks were caught in the second quarter of 2004, of which only 5% (701) were kept. Blue shark comprised 78% of the total (10,552 fish). Blue shark CPUE on tuna-targeted trips was 1.4.

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UPCOMING EVENTS

The Northwestern Hawaiian Islands Third Science Symposium

November 2-4, 2004, Hawai'i Convention Center, Honolulu
Contact: Jarad Makaiau at jarad.makaiau@noaa.gov
Online information: http://hawaiianatolls.org/sym3

Pelagic Fisheries Research Program Principal Investigators Workshop

November 29-December 1, 2004
CLIOTOP Meeting, December 1-3, 2004
Imin Conference Center, University of Hawai'i at Mānoa
Contact: John Sibert at sibert@hawaii.edu
Online information: http://www.soest.hawaii.edu/PFRP

PrepCon VII (The Preparatory Conference for the Commission for the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific)

December 6-7, 2004, Pohnpei, Federated States of Micronesia
Contact: Secretariat, Ministry of Marine Affairs and Fisheries at spica@centrin.net.id
Online information: http://www.ocean-affairs.com

Inaugural Session of the Commission

December 8-10, 2004, Pohnpei, Federated States of Micronesia
Contact: Secretariat, Ministry of Marine Affairs and Fisheries at spica@centrin.net.id
Online information: http://www.ocean-affairs.com

Marine Fisheries Advisory Committee

January 1-13, 2005, Hawai'i
Contact: Laurel Bryant at Laurel.Bryant@noaa.gov
Online information: www.nmfs.noaa.gov/mafac.htm

25th Annual Symposium on Sea Turtle Biology and Conservation

January 16-22, 2005, Hyatt Regency on the Savannah River, Savannah, Georgia
Contact: Donna Broadbent, 25th Symposium Coordinator dmarie@thezenithgrp.com
Online information: www.seaturtle.org/symposium

Integrated Modeling for Protected Species

Simon Hoyle and Mark Maunder

Managing wildlife-human interactions has become increasingly important as human influence on natural habitats has grown. To meet their objectives, managers must know the likely consequences of their actions. Fisheries modelers have developed ways to provide better advice by combining the information from multiple sources in a single model. We are applying these methods to management and conservation issues for protected species.

General Outline of Integrated Analysis

"Integrated analysis" for population dynamics and decision analysis is generally applicable, extremely flexible, uses data efficiently, and gives answers that can be applied directly to management objectives. It has been used commonly in fisheries stock assessment models for several decades, and is becoming popular in wildlife management.

It often uses Bayesian methods, which have advantages but are not essential. Bayesian analysis is itself becoming one of the most common methods for describing uncertainty in assessment of fish and marine mammals. It is also becoming popular in wildlife management.

In addition to describing uncertainty, Bayesian analysis uses "prior distributions," which can introduce information from outside the analysis. These priors can be developed from previous studies on the same or different populations, or even different species, from meta-analyses or from expert judgment.

However, priors from previous analyses have disadvantages. It may be hard to define the shape of the prior correctly; or the prior may not transfer all the information in the data. Integrating the prior analysis with the current one solves these problems.

When integrating data sources, we measure the model fit to each data set in a common currency, the likelihood, which is based on standard probability distributions. We then combine the likelihoods by multiplication. We can extend the integration beyond data alone by using priors as described above, and expressing them in terms of likelihood with respect to the model.

The combined likelihood behaves much like an individual likelihood. We can use numerical searches to maximize the combined likelihood, and standard methods of model selection. Alternatively, we can use Bayesian methods, such as Markov chain Monte Carlo (MCMC), to integrate across parameter values and model structures and to estimate posterior distributions.

Managers need advice about both the uncertainty in population status and the consequences of different management actions. Therefore, it is important to extend the analysis into the future, and to estimate outcomes for different management actions. Both expected outcome and uncertainty can be used to choose the best management strategy.

Management actions will affect both the protected species and the harvested species, so both should be considered. An integrated model in a Bayesian framework uses the data and describes the uncertainty most efficiently, and is the most rigorous method for forward projection.

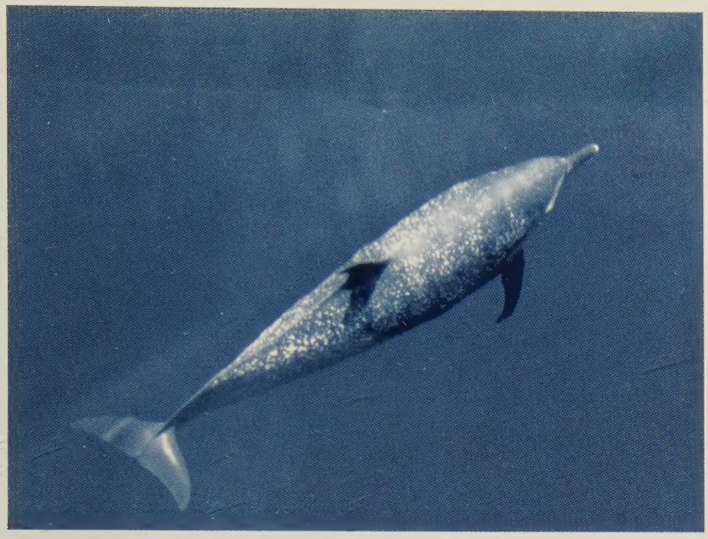
Case Studies—Dolphins and Albatrosses

Two protected species that interact with fishing operations are the northeastern Pacific stock of spotted dolphin (*Stenella attenuata*) and the Hawaiian population of black-footed albatross (*Phoebastria nigripes*). Both of these populations are of concern because they are taken as bycatch and their populations have been reduced.

Both species are the focus of conservation groups, and are of interest to the general public. Bycatch of seabirds and marine mammals is a serious problem in many other fisheries worldwide.

The tuna fishery-dolphin interaction in the eastern Pacific Ocean (EPO) is a well-known example of interactions between a protected species and a commercial fishery. The EPO tuna purse-seine fishery produces between 100,000 and 400,000 metric tons of yellowfin tuna per year, mostly from dolphin-associated schools.

Historically, a great many dolphins were killed in this fishery, and two populations are described as depleted by the U.S. govern-



ment. Pressure to reduce the dolphin mortality led to better gear and release procedures, and mortality limits that together resulted in dramatic declines in mortality.

These decisions were taken in a context of uncertainty about such important aspects of dolphin ecology as population sizes, and rates of reproduction and natural mortality. Better information would facilitate decisions that take into account costs, benefits and risks of alternative actions.

We used integrated analysis to examine the effect of bycatch mortality on the population dynamics of northeastern offshore spotted dolphin, estimate population parameters, and examine likely future population trajectories. Spotted dolphins go through a series of color phases as they grow. We used these as stages in the model.

We developed an age- and stage-structured population dynamics model and fitted it to three types of observed data: age- and stage-structure data from 1973-1978, stage-structure data from 1971 to 2000, and population size estimates from several line-transect surveys. Informative priors were also developed for some model parameters. We used MCMC to estimate the Bayesian posterior distribution. Finally, forward projections based on the posterior distribution were used to examine different management scenarios.

Results suggested that population size is now relatively stable, and gave estimates of growth rates between color phases, and lower fishing vulnerability for two of the juvenile color phases. Integrating multiple data sources was shown to improve parameter precision. There was some indication of conflicting information

(continued on page 8)

PUBLICATIONS OF NOTE

Adam, M. S., and J. R. Sibert. 2004. Use of Neural Networks with Advection-Diffusion-Reaction Models to Estimate Large-Scale Movements of Skipjack Tuna from Tagging Data. University of Hawai'i, Joint Institute for Marine and Atmospheric Research, 34 p. SOEST 04-03; JIMAR Contribution 04-350. PDF file available online: http://www.soest.hawaii.edu/PFRP/pub_list.html

Grubbs, R. D. and K. N. Holland. 2003. Yellowfin and Bigeye Tuna in Hawai'i: Dietary Overlap, Prey Diversity and the Trophic Cost of Associating with Natural and Man-made Structures. *Proceedings of the 54th Annual International Tuna Conference,* Lake Arrowhead, California, 13-16 May 2003. SWFSC, NMFS, NOAA, La Jolla, CA.

Musyl, M. K., R. W. Brill, C. H. Boggs, D. S. Curran, T. K. Kazama, and M. P. Seki. 2003. Vertical Movements of Bigeye Tuna (*Thunnus Obesus*) Associated with Islands, Buoys, and Seamounts near the Main Hawaiian Islands from Archival Tagging Data. *Fish. Oceanogr.* 12:152–169.

National Oceanic and Atmospheric Administration, the National Marine Fisheries Service's Pacific Islands Fisheries Science Center, the Pacific Islands Regional Office, and the Western Pacific Regional Fishery Management Council. 2003. *The Strategic Plan for the Conservation and Management of Marine Resources in the Pacific.* PDF file available online: http://www.wpcouncil.org

CORRECTION

Micronesia will host the Commission Secretariat and the Commission's inaugural meeting in 2005, not the Marshall Islands as previously reported.

Integrated Modeling (continued from page 7)

between data sources; we are looking into this further.

Our next analysis involves the black-footed albatross population on Tern Island, Hawai'i. This species has been assessed as vulnerable under the criteria of the International Union for Conservation of Nature and Natural Resources, based on a projected population decrease of more than 20% over three generations. We are integrating a longterm mark-recapture dataset with count data from the nesting area, and information about fishing effort and bycatch rates.

This work was funded by a grant from the Pelagic Fisheries Research Program, University of Hawai'i.

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